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SEVERE WINTER WEATHER AND BIRD POPULATIONS IN SOUTHERN ILLINOIS

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In 1973 we initiated a comparative study of bird populations in 5 mature upland and in 10 mature bottomland forests in southern Illinois, censusing the same tracts winter and summer. We censused the study areas in the winters of 1973–74, 1974–75, 1975–76, and had finished about one-half of the census in 1976–77 when heavy snow (for the region) with extreme cold covered the area on 7 January. Conditions were so severe that police stopped highway travel for several days, and we were forced to curtail our censusing. We did not resume censusing until 3 February, from which date to 18 February we completed our usual census routes and repeated all that we had done earlier in the season.

The comparison between our early and late censuses within the 1977 season and with other years provides an interesting picture of responses of bird populations to exceptional weather.

METHODS

Our strip censuses were made by 2 observers walking at a fairly constant rate (average, 2.4 km per h), counting birds that occurred within a 27.5 m-wide transect of the habitat (Graber and Graber 1963). To reduce variability in the eounts, we used marked routes in relatively large tracts, censused within a limited time period daily and seasonally, and eensused only when weather permitted suitable visibility. Total area of individual tracts censused varied from 109 ha to over 500 ha. The total area of eensus transeets in bottomland forest averaged 189.4 ha per winter, with the transect area of separate tracts averaging 19.8 ha. Upland forest transeets each winter averaged 101.6 ha, with the transects in separate traets averaging 19.8 ha. All eensuses were made between 08:00 and 16:00 CST, and between 26 December and 1 February, exeept in 1977 when the repeat eensuses extended to 18 February. In addition to the forest censuses, urban residential habitat (77.3 ha) was eensused in 3 towns—Anna, Carmi, and Mt. Vernon—in the winter of 1975–76. In the winter of 1976–77 we had time to eensus only 1 town (Metropolis), but this town was censused both before and after the severe weather. The length of our census transeets in all habitats totalled 380 km in the winter of 1976–77.

The bottomland forests we censused occupied the floodplain and the first level above, along larger streams in southern Illinois (Fig. 1, nos. 1–4, 6, 8, 10, 11, 13, 15). The trees reached a maximum diameter (DBH) of 122 cm, and there were from 1 to 8 large (over 56 cm DBH) trees per ha. The upland forests censused occupied the hilltops and ravines and had trees that reached a maximum diameter of 127 cm, with 1 to 9 large trees per ha. Genera comprising 85% (based on importance, see Lindsey et al. 1958) of the bottomland forests were *Quercus*, *Carya*, *Acer*, *Celtis*, *Ulmus*, *Fraxinus*, and *Liquidambar*. The same genera, plus 2 others—*Liriodendron* and *Sassafras*—made up 85% of the trees in the

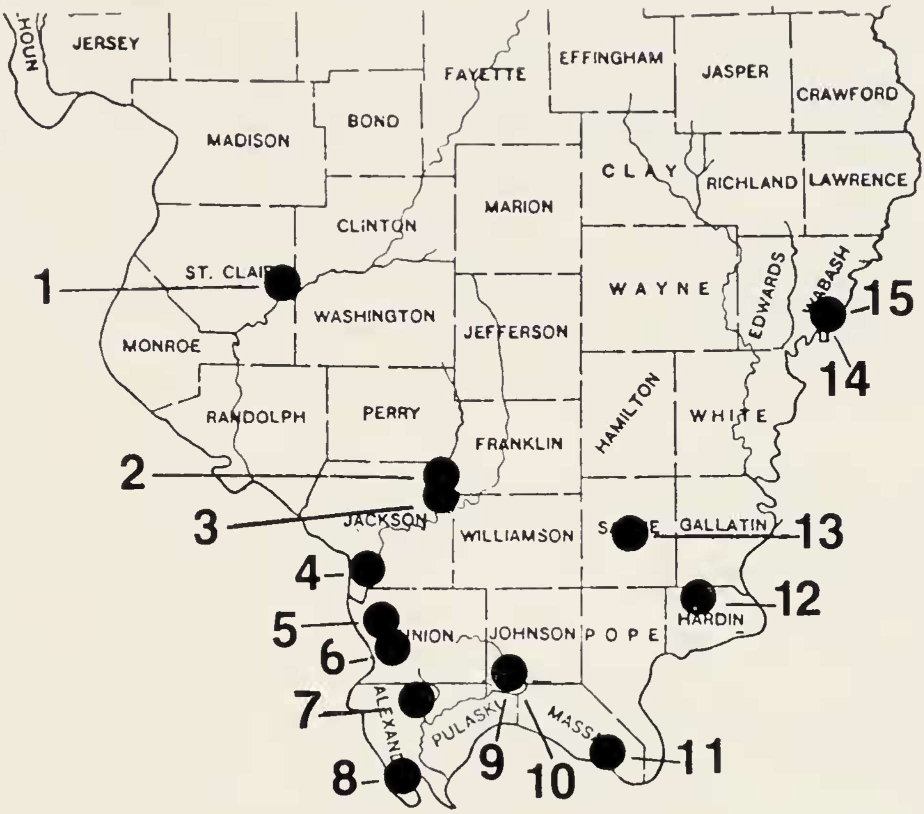

FIG. 1. Location of forest census areas in Southern Illinois. 1—Jim's Pond on the Kaskaskia River; 2, 3—Campbell Lake, Snyder Lake on the Little Muddy River; 4—Oakwood Bottoms on the Big Muddy River; 5—Pine Hills-LaRue Ecological Area; 6—Union County Conservation Area; 7—Possom Trot Trail near Elco; 8—Horseshoe Lake Island Nature Preserve; 9, 10—Heron Pond Nature Preserve, upland and bottomland on the Cache River; 11—Ft. Massac State Park on the Ohio River; 12—Kaskaskia Experimental Forest; 13—Barnes and Evans' tract on the Middle Fork of the Saline River; 14, 15—Beall Woods, upland and bottomland on the Wabash River.

upland forests censused. The difference between the uplands and bottomlands lay chiefly in topography and in the species of woody plants in the 2 habitats.

We have discussed only species encountered in the transects in 1976–77 and only those (woodpeckers and passerines) whose range of activity allows reasonable estimate of their numbers in the censused acreage by the procedure used. Other species occurring within the transects were Turkey (*Cathartes aura*) and Black (*Coragyps atrata*) vultures, Red-tailed (*Buteo jamaicensis*) and Red-shouldered (*B. lineatus*) hawks, Rock (*Columba livia*) and Mourning (*Zenaida macroura*) doves, and Great Horned (*Bubo virginianus*) and Barred (*Strix varia*) owls. We did not make systematic searches for dead birds but identified dead specimens we happened to see during the censuses.

RESULTS

The severity of the winter 1976–77 can be seen by comparing the climatological records of the previous 3 winters with those of 1976–77 (Table 1). The stations listed in Table 1 represent the longitudinal and

TABLE 1

TEMPERATURE AND DEPTH AND DURATION OF SNOW COVER AT 3 STATIONS IN SOUTHERN ILLINOIS DURING DECEMBER–FEBRUARY 1973–1977 (U.S. ENVIRONMENTAL SERVICE DATA 1973–1977)

		Nashville			Rosiclaire			Cairo		
Measurement	Year	Dec.	Jan.	Feb.	Dec.	Jan.	Feb.	Dec.	Jan.	Feb.
Maximum depth of snow on ground (cm)	1973	23			10			8		
	1974	8	5	10	2	2	0	0	T[1]	T
	1975	15	2	8	2	T	T	2	T	T
	1976	8	8	5	2	2	8	2	2	8
	1977		41	28		23	10		15	2
Number of days with 1.3 cm or more of snow on the ground	1973	8			4			2		
	1974	–	14	0	0	3	0	0	0	1
	1975	4	–	1	0	0	1	0	0	0
	1976	0	4	5	0	1	2	0	1	2
	1977		31	9		27	6		26	2
Lowest temperature for month (°C)	1973	−18.3			−16.7			−13.9		
	1974	−8.9	−19.4	−12.8	−8.3	−15.0	−10.0	−6.7	−13.9	−13.9
	1975	−13.3	−12.2	−15.5	−11.7	−12.2	−12.2	−10.5	−10.0	−10.0
	1976	−20.0	−19.4	−15.0	−20.5	−18.9	−13.9	−17.2	−15.0	−8.3
	1977		−27.8	−17.8		−26.7	−16.1		−18.3	−12.2
Average temperature for month (°C)	1973	0.5			2.2			2.9		
	1974	2.3	0.7	3.4	3.7	3.7	4.7	3.9	3.3	5.2
	1975	2.4	1.9	1.6	3.6	3.7	3.8	5.1	4.1	4.4
	1976	−1.1	−1.6	6.6	0.6	−0.3	7.7	2.1	1.6	9.5
	1977		−9.2	1.3		−7.1	2.0		−5.3	4.0

[1] Trace of snow.

latitudinal extent of all areas censused. There were very low temperatures and heavy snow cover that remained for an exceptionally long period for the region (over a month).

Overall, the bird population declined sharply during the severe weather, falling about 58% in bottomland and 66% in upland forest. By contrast there was a slight increase (9%) in the urban habitat (Table 2). Early in the winter, bird populations in both forest habitats were higher than average (bottomland, 1.4×; upland, 2.0×), but the urban habitat appeared to have lower numbers of birds than in 1975–76 (0.8×). These figures are important to understanding the population pressure on each habitat.

The decline during the winter was not uniform among species of birds. Of the 37 species in bottomland forest, 28 (73%) lost in numbers, 8 gained, and 1 remained the same (Table 2). Fourteen bottomland species lost over 50% of their early winter populations. Another 4 species of the bottomland each declined by over 40%. Of the 25 species in upland forest, 12 declined (48%) whereas 13 gained in numbers. Ten species in upland forest were each reduced by more than 50%. In urban residential habitat 7 species declined in numbers (37%) and 12 gained. Five species in this habitat lost as much as 50% of their populations.

Of the possible explanations for rather abrupt population declines, the most probable would seem to be emigration, local movement, and/or mortality. We do not believe that changing conspicuousness of birds was an important factor in the observed changes, except possibly in the case of the Pileated Woodpecker.

The reasons for changes in numbers of birds are difficult to prove, especially with unmarked populations. Only the Cedar Waxwing declined conspicuously in numbers by February 1977 without evidence of habitat change or mortality. We presumed this species to have emigrated from the area.

The majority of the observed population changes seemed to involve some shift in habitat use. Examples were the Downy Woodpecker, Red-headed Woodpecker, White-breasted Nuthatch, and Yellow-rumped Warbler, all of which appeared to have moved at least some of their population from bottomland to upland forest. Only the robin shifted from upland to bottomland forest. Crows and shrikes probably shifted from more open habitats to forest. The shrikes are particularly interesting as we have never encountered them in forest habitat before. A number of species—Red-bellied Woodpecker, Blue Jay, titmouse, chickadee, Mockingbird, robin, Starling, Purple Finch, junco, and White-throated Sparrow—showed evidence of population shift to urban residential habitat.

Some of the population decline definitely represented mortality, indicated by our finding of dead specimens on the snow. In other years we have rarely found dead birds while censusing; the method is ill-designed for finding them, as the observer's attention is focused away from his own proximity. Thus, the finding of any dead birds may be indicative of high mortality, and the fact that we found no dead of some species should not be construed as an absence of mortality. All specimens we found were on top of the snow. Birds that died during the blizzard would have been covered. In February 1977 we found the remains of 6 flickers, 1 Pileated Woodpecker, 2 immature and 1 adult Red-headed Woodpeckers, 2 Downy Woodpeckers, 4 Blue Jays, 4 titmice, 2 Carolina Wrens, 1 Brown Thrasher, 4 robins, 2 bluebirds, 2 kinglets, 2 Yellow-rumped Warblers, 3 red-wings, 9 grackles, 3 Cardinals, 1 Purple Finch, 4 towhees, 6 juncos, 1 Tree Sparrow, and 3 white-throats. Besides carcasses we found numerous flight feathers, especially from flickers and immature Red-headed Woodpeckers.

TABLE 2

WINTER BIRDS PER 40.5 HA IN MATURE BOTTOMLAND AND UPLAND FOREST AND URBAN RESIDENTIAL HABITAT IN SOUTHERN ILLINOIS BEFORE AND AFTER SEVERE WINTER WEATHER IN JANUARY 1977, PLUS THE AVERAGE DENSITY FOR THE PRECEDING 3 WINTERS (1974–76)

Species	Bottomland forest				Upland forest				Urban residential			
	1977		1977 % change	3-year mean	1977		1977 % change	3-year mean	1977		1977 % change	1975–1976
	Dec.–Jan.	Feb.			Dec.–Jan.	Feb.			Dec.–Jan.	Feb.		
Yellow-shafted Flicker (*Colaptes a. auratus*)	11.9	4.6	–61.3	5.4	1.1	0.9	–18.2	2.6	5.1	3.2	–37.3	1.0
Pileated Woodpecker (*Dryocopus pileatus*)	0	3.6	+	0.9	0	0.4	+	0.2	0	1.6	+	0.5
Red-bellied Woodpecker (*Melanerpes carolinus*)	8.9	8.7	–2.2	9.4	15.0	6.4	–57.3	6.5	1.3	4.7	+261.5	5.2
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	79.6	47.5	–40.3	34.2	3.2	19.7	+515.6	8.4	0	0	0	0.5
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	3.0	0.8	–73.3	1.6	0	0.4	+	0.4	3.8	1.6	–57.9	1.6
Hairy Woodpecker (*Picoides villosus*)	1.7	1.7	0	0.9	0	0.4	+	0.9	0	0	0	2.1
Downy Woodpecker (*Picoides pubescens*)	15.3	8.2	–46.4	13.7	2.1	3.8	+80.9	5.6	3.8	0	–100	3.7
Blue Jay (*Cyanocitta cristata*)	15.3	10.8	–29.4	11.6	9.7	9.8	+0.1	5.1	17.9	31.6	+76.5	31.9
Common Crow (*Corvus brachyrhynchos*)	1.3	3.2	+146	2.7	0	5.6	+	0.1	0	0	0	0
Carolina Chickadee (*Parus carolinensis*)	24.3	11.6	–52.3	14.6	8.6	9.4	+9.3	5.0	0	1.6	+	4.2

TABLE 2 (continued)

Species	Bottomland forest				Upland forest				Urban residential			
	1977 Dec.–Jan.	1977 Feb.	1977 % change	3-year mean	1977 Dec.–Jan.	1977 Feb.	1977 % change	3-year mean	1977 Dec.–Jan.	1977 Feb.	1977 % change	1975–1976
Eastern Tufted Titmouse (*Parus b. bicolor*)	24.7	12.5	-49.4	27.3	12.9	13.7	+6.2	13.8	0	1.6	+	0.5
White-breasted Nuthatch (*Sitta carolinensis*)	3.0	1.7	-43.3	2.3	0	2.1	+	4.6	0	0	0	0
Brown Creeper (*Certhia familiaris*)	3.8	3.2	-15.8	3.0	2.1	1.3	-38.1	1.1	0	0	0	0
Winter Wren (*Troglodytes troglodytes*)	0.8	0	-100	1.7	0	0	0	0	0	0	0	0
Carolina Wren (*Thyrothorus ludovicianus*)	4.3	0	-100	4.0	0	0	0	1.8	0	0	0	2.6
Mockingbird (*Mimus polyglottos*)	0	0	0	0.1	0	0	0	0	1.3	11.1	+753.8	5.7
Brown Thrasher (*Toxostoma rufum*)	3.8	0.6	-84.2	0.6	0	0	0	0	0	0	0	1.0
American Robin (*Turdus migratorius*)	10.6	14.8	+40	11.2	61.3	6.0	-90.2	20.9	0	14.2	+	12.5
Hermit Thrush (*Catharus guttatus*)	0	0	0	1.0	3.2	0	-100	0.5	0	0	0	0
Eastern Bluebird (*Sialia sialis*)	2.5	0.4	-84	4.2	8.6	0.9	-89.5	2.2	0	0	0	0
Golden-crown Kinglet (*Regulus satrapa*)	5.5	0	-100	7.4	4.3	0	-100	5.4	0	0	0	0

TABLE 2 (continued)

Species	Bottomland forest				Upland forest				Urban residential			
	1977		1977		1977		1977		1977		1977	
	Dec.–Jan.	Feb.	% change	3-year mean	Dec.–Jan.	Feb.	% change	3-year mean	Dec.–Jan.	Feb.	% change	1975–1976
Ruby-crowned Kinglet (*Regulus calendula*)	1.3	0	–100	0.8	0	0	0	0.4	1.3	0	–100	0
Cedar Waxwing (*Bombycilla cedrorum*)	12.8	0	–100	0	78.5	0	–100	0	0	0	0	0
Loggerhead Shrike (*Lanius ludovicianus*)	0.8	0.2	–75	0	0	0.4	+	0	0	0	0	0
Starling (*Sturnus vulgaris*)	2.1	0	–100	3.9	9.7	0	–100	0.5	506.0	650.1	+28.5	688.3
Yellow-rumped Warbler (*Dendroica c. coronata*)	6.8	0.6	–91.2	4.6	3.2	5.1	+59.4	1.4	0	0	0	1.0
House Sparrow (*Passer domesticus*)	0	0	0	0	0	0	0	0	198.6	204.0	+2.7	302.1
Red-winged Blackbird (*Agelaius phoeniceus*)	11.9	10.6	–10.9	13.8*	0	0	0	0	0	0	0	0
Rusty Blackbird (*Euphagus carolinus*)	0.8	0.2	–75	11.4	0	0	0	0	0	0	0	0
Common Grackle (*Quiscalus quiscula*)	25.5	20.7	–18.9	28.2*	0	0	0	2.2	161.4	53.8	–66.7	2.6
Cardinal (*Cardinalis cardinalis*)	22.6	5.9	–73.9	23.8	6.4	3.0	–53.1	7.3	38.4	38.0	–1.0	30.8

* 2-year average (1974–75 and 1975–76).

TABLE 2 (continued)

Species	Bottomland forest				Upland forest				Urban residential			
	1977		1977 % change	3-year mean	1977		1977 % change	3-year mean	1977		1977 % change	1975–1976
	Dec.–Jan.	Feb.			Dec.–Jan.	Feb.			Dec.–Jan.	Feb.		
Purple Finch (*Carpodacus purpureus*)	0.4	0.2	–50	1.6	8.6	0	–100	0.3	1.3	9.5	+630.8	0
American Goldfinch (*Carduelis tristis*)	4.7	7.8	+66	13.0	0	0.4	+	1.0	0	0	0	3.7
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	17.4	2.1	–87.9	1.9	0	0	0	0.2	0	0	0	0
Slate-colored Junco (*Junco h. hyemalis*)	25.5	4.4	–82.8	25.4	37.6	5.1	–86.4	34.1	30.7	33.2	+8.1	74.2
Tree Sparrow (*Spizella arborea*)	0	1.7	+	7.4	0	0	0	1.9	0	0	0	0
Field Sparrow (*Spizella pusilla*)	3.0	0	–100	0.7	0	0	0	1.0	3.8	0	–100	7.8
White-throated Sparrow (*Zonotrichia albicollis*)	99.6	0.3	–99.7	29.4	0	0	0	0.3	0	4.7	+	0.5
Swamp Sparrow (*Melospiza georgiana*)	0	0.2	+	3.4	0	0	0	0	0	0	0	0
Song Sparrow (*Melospiza melodia*)	0	0.4	+	2.7	0	0	0	0.2	0	0	0	7.3
Total birds per 40.5 ha	455.5	189.2	–58.5	329.8	276.1	94.8	–65.7	135.9	974.7	1064.5	+9.2	1191.3
Total ha censused	95.1	191.6		188.5	37.6	94.5		104.1	31.6	25.6		77.4

In the case of the Hermit Thrush, the 2 wrens, the 2 kinglets, and the Field Sparrow we believe there was 100% mortality. There was also very high mortality in the flicker, Brown Thrasher, bluebird, Cardinal, towhee, junco, and White-throated Sparrow. In addition, we suspect that there was more mortality than might be expected of Red-bellied Woodpeckers, sapsuckers, and Brown Creepers. The expected winter mortality is unknown and undoubtedly varies from species to species. Lack (1966) recorded winter-to-spring mortality of 31–75% in the Great Tit (*Parus major*) in different years, with the highest mortality in a severe winter. It should be remembered that the losses described in this paper represent only 1 month and not the whole winter season.

DISCUSSION

Interpretation of changes in densities of populations as mobile as birds is particularly difficult, and studies that deal with single habitats may be especially misleading. Our study, which included only arboreal habitats, indicated a decline of 61% in the flicker population in bottomland forest, an 18% loss in upland forest, and a 37% loss in residential habitat. The available evidence (large numbers of dead specimens) suggests that these losses represent mortality. Our earlier studies on Illinois populations (Graber and Graber 1963) indicate that arboreal habitats hold only about 3% of the total flicker population in southern Illinois in winter. We might assume that mortality in more open habitats was at least as great, but the problem is more complicated than that, as some populations moved from more open habitats to forest, and what we construed as 61, 18, or 37% mortality may have been much greater, because our before-and-after density figures do not account for birds that may have moved into the habitat and died in the period between the counts.

In assessing population losses and gains, one must also take into account the available areas of habitats. Our study areas were chosen for maturity and large area size and are not strictly representative of southern Illinois forests in general, but populations in other forests were probably at least as vulnerable as those we observed. We have estimated that there are about 218,535 ha of bottomland forest, 517,321 ha of upland forest, and 122,865 ha of residential habitat in southern Illinois (Graber and Graber 1976). At the observed densities for these habitats we could estimate that there were, for example, about 241,400 Carolina Chickadees before the severe weather and 187,000 after (including about 4900 in urban habitat), a net loss of about 22% for the month. The great loss in bottomland forest was somewhat counterbalanced by smaller increases in upland forest, because the area of upland forest is more than twice as great as the bottomland. If we assume the observed density changes represent emigration, the possibility of mortality is still not eliminated. Conditions as bad or worse than those that prevailed in southern Illinois existed several hundred km in all directions. If a bird cannot survive where it knows the resources, moving to an unknown and probably already occupied area is not likely to improve the situation and involves an energy cost that increases with distance.

We believe that most of the observed density changes that were not the result of mortality represented only local movements by birds in search of special food situations. Thus, Yellow-rumped Warblers virtually disappeared from bottomland forests (their preferred winter habitat) and became numerous in certain upland forests that had an abundance of poison ivy (*Rhus radicans*) fruits. Early in the winter we found flocks of robins feeding on the fruit of shining sumac (*R. copallina*) and greenbrier (*Smilax bona-nox*) in upland forests. In February the uplands were bare of these fruits and robin flocks were congregating to feed on persimmons (*Diospyros virginiana*) in bottomland forests. A late frost in May 1976 retarded the development of persimmons so that these fruits remained on the branches and were thus available when snow covered the ground. The same freeze also retarded the development of acorns in the upland forests so that many acorns were also still on the branches in February; they were probably the reason for the shift of Red-headed Woodpeckers from the bottomland forests to the upland.

Interspecific competition is probably accentuated with severe weather. Red-headed and Red-bellied woodpeckers are both mast feeders, and their populations show a consistent inverse relationship in Illinois in winter (Graber et al. 1977). In southern Illinois red-head populations are correlated positively with alternate-year highs in the acorn crop. The highs in recent decades have occurred in (January) the odd-numeral years, and 1977 was typically high with an exceptionally large population of red-heads. The red-head population is usually concentrated in bottomland forest. Red-bellies also show a preference for bottomland forest, but in years with high densities of Red-headed Woodpeckers, red-bellies are apparently unable to compete and move to upland forest, as they did in the winter of 1976–77 (Table 2). When snow covered the mast crop, red-heads moved to those upland areas where acorns remained on the trees. This move probably saved much of the red-head population but may have increased mortality of red-bellies, which, overall, lost more than 40% of their population.

A notable pattern in the data was the similarity of population changes in related species. For example, parids declined at similar rates in bottomland forest while increasing at similar rates in upland forest and urban habitat:

wrens and kinglets showed a total loss; and thrushes all lost heavily in upland forest. The observation implies consistent responses to stress by congeners among a wide range of species and perhaps a tendency to compete for the same resources. Population shifts between habitats by a species were invariably from habitats with high population density to those with lower density.

Certain species seem to be especially vulnerable to severe winter weather and have a history of population crashes. Included here are most of the species in which we observed a 100% decline. Population declines of the Carolina Wren in winter have been discussed by Bent (1948) and James (1961), and of bluebirds and Hermit Thrushes by James (1959, 1960, 1961, 1962). Bent (1949) mentioned possible mortality of Golden-crowned Kinglets in severe winters but not of Ruby-crowned Kinglets.

The disadvantage of heavy snow cover to ground foragers is evident, as 9 of the 11 species that suffered declines above 80% are ground foragers (e.g., Brown Thrasher, Winter Wren, towhee, junco).

Small size was also a great disadvantage (Fig. 2), with kinglets being particularly vulnerable and the only aboveground (arboreal) foragers to show a total loss.

Within a species, the inexperienced immature birds, and possibly also the aged and infirm, suffered the greatest losses. Two of the 3 Red-head specimens we found were immatures, and, in addition, we found a number of immature tertials from red-heads that may have died, though the feathers could also have been molted. Increased mortality of immatures in severe weather has been observed in the Great Tit by Lack (1966).

Birds near the northern limits of their winter range probably suffer the greatest losses when a severe winter occurs. Southern Illinois is near the northern limit of regular winter occurrence for some of the species that suffered high losses (e.g., Brown Thrasher, Hermit Thrush, Ruby-crowned Kinglet, Yellow-rumped Warbler).

Some birds survived the severe weather because of food provided by man. Bird feeders and special plantings in town were part of the reason bird populations increased in urban habitat (e.g., an 8-fold increase in Mockingbirds). Some ground foragers that survived (white-throats and juncos are examples), survived mainly in the urban habitat, and urban Cardinals apparently survived better than those in the natural habitats (Table 2). The only Swamp Sparrows we found after the blizzard were in bottomland woods near a large cattle-feeding station, where food in the form of silage, grain, and grass seed from hay was available.

Certain of our observations appear to exemplify an important biological principle—that mortality in times of crisis is directly proportional to what

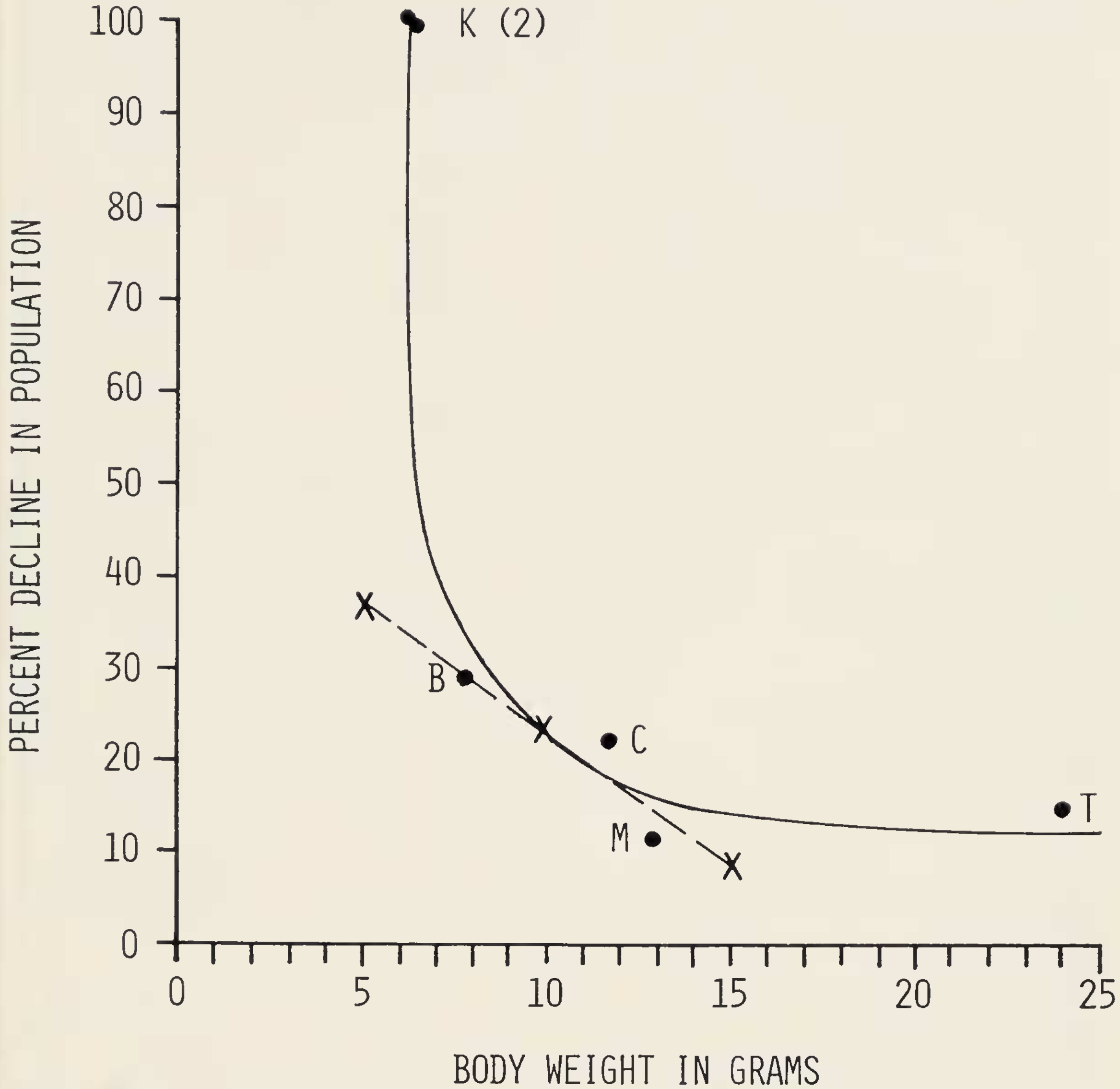

FIG. 2. Relationship between population loss and body weight of smaller species censused. Only arboreal foragers are included, as follows: K (2)—Golden-crowned and Ruby-crowned kinglets; B—Brown Creeper; C—Carolina Chickadee; M—Yellow-rumped Warbler; T—Tufted Titmouse. Weights are averages for 2 or more winter specimens. Dashed line represents calculated regression of population loss on weight for the 3 middle-range species ($r = 0.916$). The curve was estimated by eye.

could be called population pressure. A simple expression of that pressure is the total number of animals, or more precisely the biomass, and the variety of species, which, in effect, projects the influence of the mass. Bottomland forest characteristically supports more birds and more species than upland, in both respects absorbing more pressure on its resources per unit of area. Even lacking precise knowledge of what all the resources are, we can still presume that for bird populations at least, bottomland forest has more resources to exploit than upland, because of the bottomland's consistently higher, more varied population. For the fauna considered here, respective figures for the 3-year counts of species and the 3-year average of numbers of birds per 40.5 ha (100 acres) are: bottomland forest—37 species, 330 birds; upland forest—31 species, 136 birds. These average figures may represent about what the 2 habitats can support in winter over the years (that is, carrying capacity) for the usual range of conditions—weather, food supplies, and other basic needs. With the extraordinary climatic conditions of January 1977 closing off some of the (especially ground) resources, and at the same time increasing demand, not even the "usual" populations could have been sustained. We might assume that bottomland, having the most to lose (the highest population pressure), would lose more population than upland, but examination of the data (Table 2) reveals that bottomland forest lost about 58% and upland forest 66% of their populations, respectively. The losses are not related just to population pressure but to the amount of that pressure in relation to the carrying capacity of the habitat. Before the severe weather set in, bottomland with 455 birds had 38% more population than its (average) carrying capacity, whereas upland with 276 birds had 102% more than its capacity and consequently lost more. The data for urban habitat further substantiate the "mortality"-carrying capacity relationship. Early in winter the urban habitat (a consistently high-density habitat) had 975 birds per 40.5 ha, a number 18% below the capacity for the habitat, and in contrast to both the natural habitats, urban habitat actually gained (9%) in population during the winter.

What is true of the population in general is also true of the individual species. Considering the number of variable factors that affect the rate of population decline in different species during an adverse winter, it is remarkable that any single factor, such as population density, would show correlation with the decline. Yet the relationship between high population and high loss is so pronounced that a significant correlation ($r = 0.882$, Fig. 2) shows through the large specific differences in susceptibility, size, food habits, and similar factors. The graph was constructed by averaging the percentage losses of species falling in different categories of abundance.

The greater the number of birds of a species above the 3-year winter average, the greater the loss in both upland and bottomland forests (Fig. 3) during the winter of 1976–77. The Tufted Titmouse had 0.9× the average in early winter and its numbers declined 49% by February. The Brown Thrasher had 6.3× more than average and its losses were 89.5%. This relationship between abundance and amount of decline in numbers suggests that there is a limit to the number of birds of a species that can expect to obtain a survival level of sustenance in a given habitat. When numbers

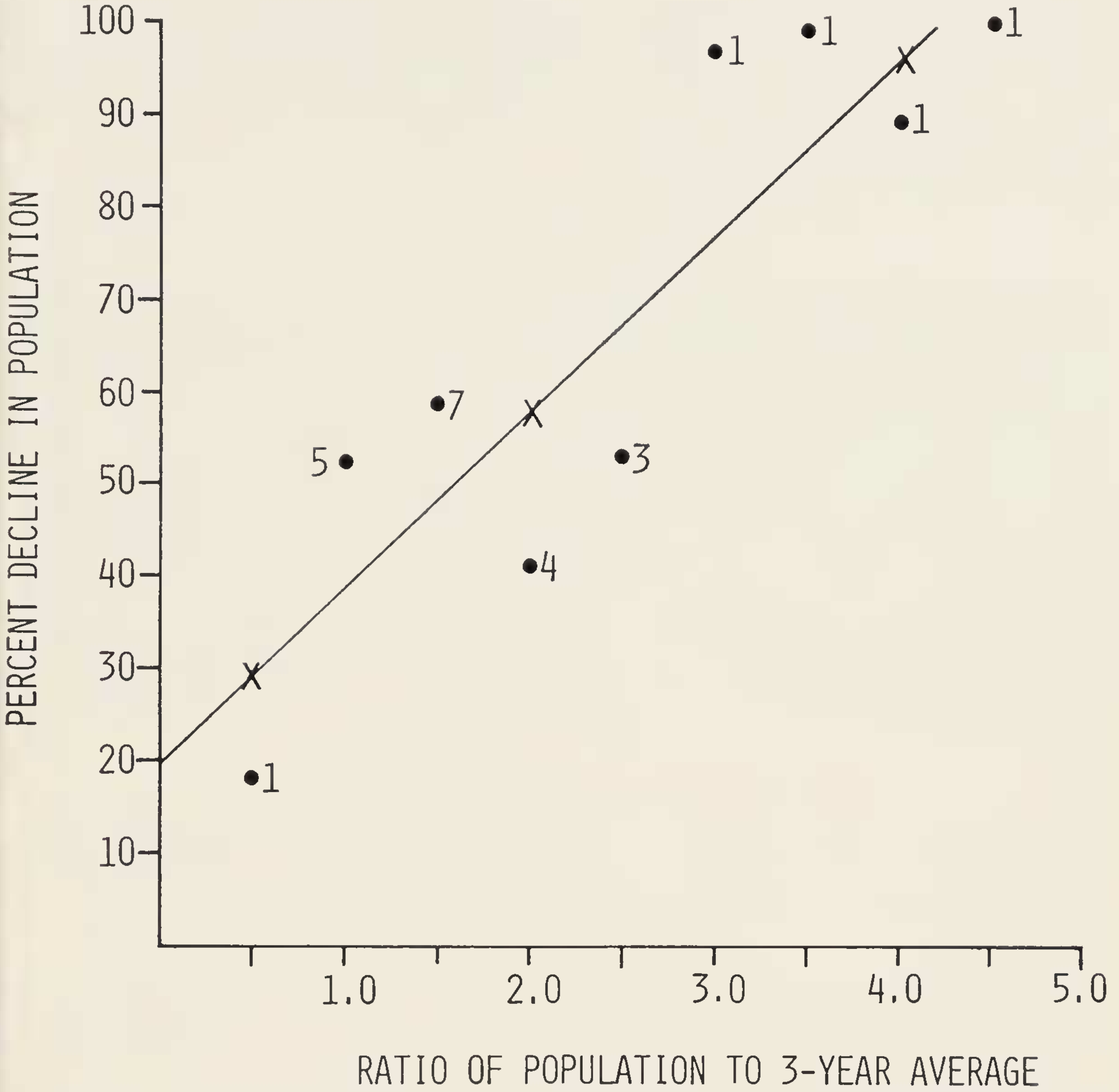

Fig. 3. Relationship of population decline in species of forest birds to their abundance in early winter, expressed as a ratio of the average winter population in the 3 preceding years (that is, 1.0 = average, 2.0 = twice the average). The numerals beside the points indicate the number of species represented by the point. Graph line is the calculated regression of population density on population loss.

exceed this level, mortality, dispersal, or both, reduce the surplus to sustainable populations. Given the initial population, the decline is predictable—the larger the population above carrying capacity, the greater the decline.

Bird populations are made up of individuals whose range of structure and behavior allows for maximum exploitation of resources and rapid adaptation to changing climatic conditions. Mild winter weather encourages the segment of a migratory species that is less inclined to migrate, whereas severe weather eliminates such birds. Mild winters may also allow northward expansion of species of southern origin, whereas inclement winters may result in a retraction of the range of such species. As Tramer (1974) has stated, winter range probably represents adaptation at the species population level to winter events that have a significant probability of occurring each winter in a given geographic region.

SUMMARY

A study was made of bird populations in 3 arboreal habitats—bottomland forests, upland forest, and urban, in southern Illinois, comparing the severe winter of 1976–77 with milder winters of the 3 previous years. Prolonged severe cold, and snow cover caused massive population shifts, and high mortality among several species of birds. Populations of certain species left their preferred winter habitats to use special food sources elsewhere. Mortality was particularly high among ground foragers, but mortality rate was also related to body size, smaller species showing the greatest decline. Closely related species showed very similar patterns of population change. Some populations survived better in urban habitat than in natural habitats probably because of food provided by humans. Population declines in a habitat were related to: (1) the initial winter population density, and (2) the carrying capacity of the habitat as expressed in the average population density for the habitat during more normal winters. The higher the population was above average, the greater the loss.

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